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Factors controlling phytoplankton ice-edge blooms in the marginal ice-zone of the northwestern Weddell Sea during sea ice retreat 1988: field observations and mathematical modelling

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Abstract. The factors controlling phytoplankton bloom development in the marginal ice zone of the northwestern Weddell Sea were investigated during the EPOS (Leg 2) expedition (1988). Measurements were made of physical and chemical processes and biological activities associated with the process of ice-melting and their controlling variables particularly light limitation mediated by vertical stability and ice-cover, trace metal deficiency and grazing pressure. The combined observations and process studies show that the initiation of the phytoplankton bloom, dominated by nanoplanktonic species, was determined by the physical processes operating in the marginal ice zone at the time of ice melting. The additional effects of grazing pressure by protozoa and deep mixing appeared responsible for a rather moderate phytoplankton biomass (4 mg Chl $a\,m^{-3}$) with a relatively narrow geographical extent (100–150 km). The rôle of trace constituents, in particular iron, was minor. The importance of each factor during the seasonal development of the ice-edge phytoplankton bloom was studied through modelling of reasonable scenarios of meteorological and biological forcing, making use of a one-dimensional coupled physical-biological model. The analysis of simulations clearly shows that wind mixing events – their duration, strength and frequency – determines both the distance from the ice-edge of the sea ice associated phytoplankton bloom and the occurrence in the ice-free area of secondary phytoplankton blooms during the summer period. The magnitude and extent of the ice-edge bloom is determined by the combined action of meteorological conditions and grazing pressure. In the absence of grazers, a maximum ice-edge bloom of 7.5 mg Chl $a\,m^{-3}$ is predicted under averaged wind conditions of 8 $m\,s^{-1}$. Extreme constant wind scenarios (4–14 $m\,s^{-1}$) combined with realistic grazing pressure predict maximum ice-edge phytoplankton concentrations varying from 11.5 to 2 mg Chl $a\,m^{-3}$. Persistent violent wind conditions ($\geqslant$ 14 $m\,s^{-1}$) are shown to prevent blooms from developing even during the brightest period of the year.

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The Antarctic sea ice zone constitutes, through sea ice retreat and advance, a key component of the Southern Ocean dynamics, both with regards to energy transfer between atmosphere and ocean and to food-web dynamics. The major role played by ice-cover and the water column turbulence on the development of phytoplankton bloom has been demonstrated by numerous field studies. As a general trend, deep-mixed ice-free areas are not exceptionally productive despite high nutrient availability, and are dominated by nanoplanktonic communities (El-Sayed, 1984; Hayes et al. 1984; Smetacek et al. 1990). On the other hand, various lines of evidence (Smith and Nelson 1985, 1986; Sullivan et al. 1988; Comiso et al. 1990) indicate that the circumpolar marginal ice zone is a region of enhanced primary production owing to the formation, at the time of ice melting, of a shallow vertically stable upper layer as a result of the production of meltwater and its subsequent seeding by actively growing sea ice microbes (Garrison et al. 1987). However, species composition and maximum biomass reached by ice-edge blooms are greatly variable within the circumpolar marginal ice zone. Nanoplanktonic forms and moderate biomasses ($<$ 10 mg Chl $a\,m^{-3}$) are typical for the Weddell Sea sector (Nelson et al. 1987; Hewes et al. 1985, 1990; Becquevort et al. 1992) whilst dramatically high biomasses of microplankton ($>$20 mg Chl $a\,m^{-3}$) have occasionally been reported in the Ross Sea (Smith and Nelson, 1985; Nelson and Tréguer 1992) and in Prydz Bay (Goeyens and Dehairs 1993).

The spatial and temporal extent of phytoplankton ice-edge blooms as well as the mechanisms controlling their wax and wane are still poorly understood. It is now agreed that vertical stability of the surface waters is the necessary condition for initiating phytoplankton ice-edge blooms

and several hypotheses on factors controlling the magnitude of these blooms have been proposed. The current debate focuses essentially the three following hypotheses. First, it has been suggested that the rapid degradation of the meltwater lens at its seaward edge by deep vertical mixing due to violent winds prevailing in this extreme environment prevents phytoplankton cells from growing under optimal light conditions (Smith and Nelson 1985; Holm-Hansen et al. 1977; Sullivan et al. 1988). The magnitude of the phytoplankton bloom thus depends in this case on the persistence of the vertical stability. However, recent studies in the marginal ice zone of the Weddell Sea (Nelson et al. 1987; Veth et al. 1992) report low phytoplankton concentration in areas exhibiting near-surface stability. Recently, trace metals deficiency, particularly iron, has been suggested as an alternative explanation for low phytoplankton concentrations in the ice-free areas of the Southern Ocean (Martin and Fitzwater 1988; Martin et al. 1990). Finally, grazing pressure by meso- (Stretch et al. 1988; Smetacek et al. 1990) or micro- (Hewes et al. 1985) zooplankton has been mentioned as the major biological factor controlling phytoplankton development along the receding ice-edge. These three hypotheses are not mutually exclusive and the importance of each may vary with location, time and environmental conditions (Nelson and Smith 1991). Based on climatological and observational forcing of simple one-dimensional ecosystem models, Mitchell et al. (1991) and Sakshaug et al. (1991) concluded indeed that phytoplankton bloom development in the Southern Ocean was governed by both physical and biological parameters that determine vertical mixing and phytoplankton loss rate.

One of the main objectives of the EPOS expedition in the marginal ice zone of the northwestern Weddell Sea during the ice retreat of 1988 was to address these issues. Our approach combined field observations, shipboard process-oriented studies and mathematical modelling. Experimental studies involved a suite of detailed measurements of the chemical transformations and biological processes associated with the ice retreat, focusing on their controlling factors (Hempel et al. 1989). Among the latter, environmental light and temperature (Lancelot et al. 1991), grazing pressure (Björnsen and Kuparinen 1991; Schalk 1991), inorganic major nutrients (Goeyens et al. 1991), as well as trace constituents (de Baar et al. 1990; Buma et al. 1991) were separately considered through field and shipboard experiments.

In this paper we first present a comprehensive synthesis of the observations and experiments, followed by an analysis through mathematical simulation of all relevant physical, chemical and biological processes. The objective is to delineate the key factors controlling phytoplankton ice-edge bloom (onset, magnitude and duration) as well as its spatio-temporal variability during its seasonal development in this particular area of the Southern Ocean.

Material and methods

Four North-South sections of four days each were completed along the 49°W meridian between 26th October and 31st December 1988 in the marginal ice zone of the northwestern Weddell Sea. The sections extended from latitudes 57°S to 62°S (Fig. 1). Data collection and water sampling for physical, chemical and biological measurements, as well as shipboard experiments, were conducted at each half degree of latitude using a teflon-coated ultraclean CTD/Rosette combination. The methods used have been described extensively in various published independent studies. Briefly they are the following:

Physical and optical measurements

Salinity and temperature profiles were determined with a Neil Brown Mark IIIb CTD-profiler (EG & G Ocean Products). In situ temperature and salinity calibrations were conducted regularly. Incident Photosynthetically Available Radiation (PAR) was continuously measured using a cosine Li-Cor sensor on the upper deck of the ship. Losses due to sea and snow-ice albedo, were calculated, on average, to be 0.15 and 0.95 respectively. The vertical light attenuation coefficient was determined from light profiles measured with an underwater quantum meter (Magas and Svansson 1989). Ice-coverage was estimated by visual observations (Van Franeker 1989).

Inorganic nitrogen and biomasses

Nitrate + nitrite was measured with a Technicon Autoanalyser II according to Tréguer and Le Corre (1975). Nitrate depletions were calculated from the vertical distribution of nitrate concentration and integrated down to the depth where nitrate reaches the winter value of 31.5 mmol m^{-3} (Goeyens et al. 1991). Chlorophyll *a* was determined by spectrofluorometry (Jacques and Panouse 1991). Average Chl *a* concentrations in the homogeneous upper layer were calculated from the vertical distribution of Chl *a*. The homogeneous upper layer depths were determined from CTD casts (Veth 1991). Samples for phytoplankton and protozoan carbon biomass calculation were preserved either with glutaraldehyde 25% (final conc. 0.5%) or with a glutaraldehyde-lugol cocktail (35‰, v/v; final conc. 1%), the choice of preservative being made according to the size and trophic mode of micro-organisms (Becquevort et al. 1992). Carbon biomass was calculated from cell counts and cell volume measurements under either an epifluorescence microscope (auto- and heterotrophic flagellates) after DAPI (4'6 diamino-2-phenylindole) staining (Porter and

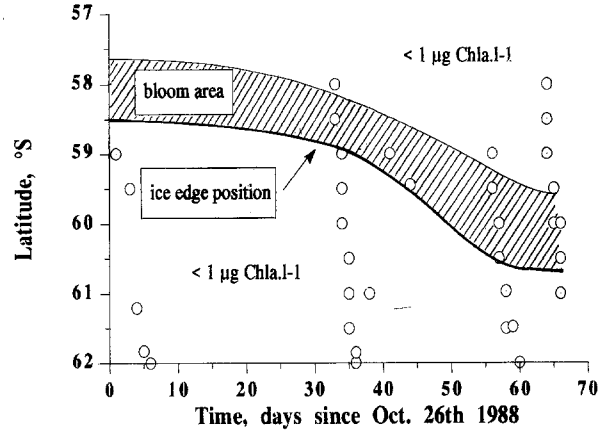

Fig. 1. Retreat of sea-ice during the 1988 EPOS expedition, the hatched area representing the zone where ambient levels of Chl *a* exceeded concentrations of 1 mg · m^{-3}. The sampled stations (o) are situated along the 49°W meridian or the 47° W meridian. Ice data courtesy Van Franeker (1989), Chlorophyll *a* data after Jacques and Panouse (1991)

Feig 1980) or an inverted microscope (diatoms and ciliates), by using appropriate carbon/cell volume conversion factors of 0.11 pgC · μm^{-3} (Edler 1979) for flagellates (auto- and heterotrophic) and diatoms, and 0.08 pgC · μm^{-3} (Beers and Steewart 1970) for ciliates. Autotrophs were discriminated from heterotrophs by their red chlorophyll autofluorescence. Details concerning this procedure are extensively described by Becquevort et al. (1992).

Biological activities

Daily phytoplankton growth was calculated using the protocols of Lancelot et al. (1989, 1990) from data on phytoplankton ^{14}C assimilation rates in combination with the knowledge of daily light variations with depth. The experimental procedure, involving measurement of short-term ^{14}C fixation rates at different light intensities and long-term (24 hours) light-dark kinetics of ^{14}C assimilation into four distinct pools of cellular constituents (proteins, lipids, polysaccharides, small metabolites), and the calculation method are extensively described in Mathot et al. (1992). Potential ingestion rate of protozoa on algal cells was estimated from protozoan abundance and biovolume measurement, as well as phytoplankton biomass, using the maximum volume-specific clearance rate (10^5 protozoan body volume h^{-1}), experimentally established by Björnsen and Kuparinen (1991). Long-term (8-12 days) Fe-enrichment experiments were performed on board under controlled clean conditions on plankton communities originating from the various physical and ice conditions prevailing in the area (de Baar et al. 1990, Buma et al. 1991).

Results and discussion

Field observations

Phytoplankton development and the receding ice-edge. In 1988, the marginal ice zone along the meridian 49°W extended from 58.5 to 61°S, a distance of about 300 km. Sea ice retreat, initiated in early November, was complete in late December (Fig. 1) and proceeded at an average rate of 5.5 km day^{-1}. In this area, the ice-edge does not retreat further South than 61°S owing to a continuous supply of sea ice from the Weddell Gyre (Ackley 1981). Maximum chlorophyll *a* concentrations of about 4 mg m^{-3} were systematically recorded at some distance of about 50 km north of the ice boundary (Fig. 1) and coincided with nitrate concentration minima (about 20 mmole m^{-3}). Moreover, a 100 to 150 km wide belt of relatively elevated phytoplankton biomass (>2 mg Chl *a* m^{-3}) was strongly associated with the receding ice-edge and moving southwards parallel with it (Fig. 1). On both sides of the region of enhanced primary production, mean chlorophyll *a* concentrations were very low (0.4 mg Chl *a* m^{-3}), reaching at times a maximum of 1 mg m^{-3}. The strong relationship between the receding sea ice and phytoplankton bloom development can be seen in Fig. 2 which shows synoptic distributions of ice-cover, averaged chlorophyll *a* concentrations over the upper wind mixed layer, and nitrate depletions (the amount of nitrate removed from the water column by phytoplanktonic uptake during the ongoing growth season) observed or calculated over a one-month interval. During this period, sea ice retreated over a distance of 270 km (Fig. 2a). Accordingly, the peak of phytoplankton shifted from 58.5 to 60°S (Fig. 2b), at a

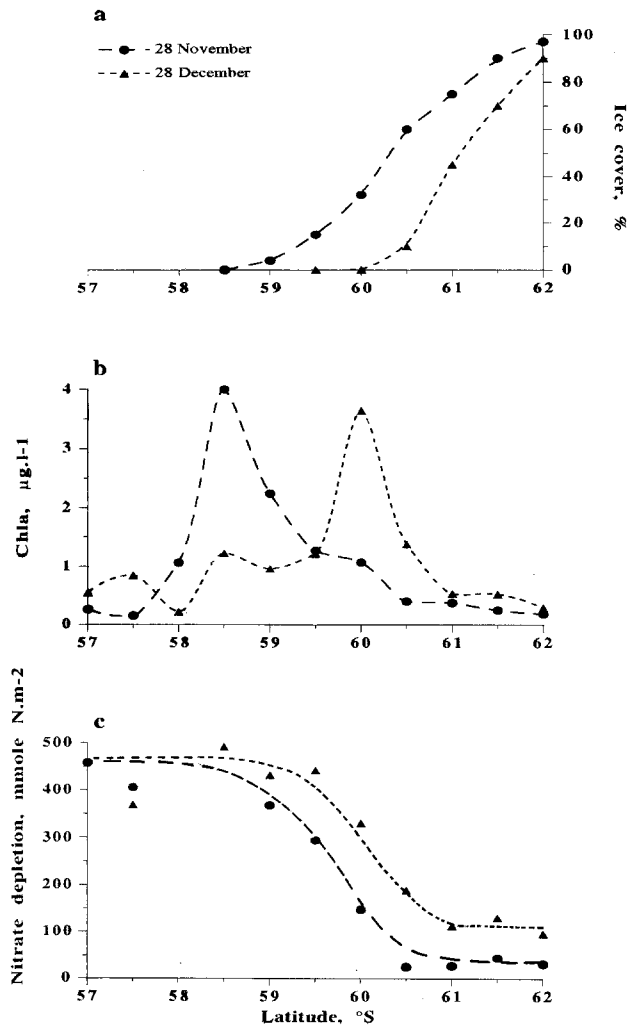

Fig. 2a–c. The retreat within one month of the ice-edge zone along the 49°W meridian: (**a**) ice-over percentage; (**b**) chlorophyll *a* concentration averaged over the upper mixed layer (after Jacques and Panouse, 1991) and (**c**) nitrate depletion (after Goeyens et al. 1991)

similar rate as the receding ice-edge (about 9 km day^{-1} during this period). Nitrate depletions (Fig. 2c) reached a maximum of 500 mmole N m^{-2} and closely followed the sea ice retreat. The two phytoplankton blooms (Fig. 2b) were similar, in magnitude as well as in extent, suggesting that their controlling mechanisms were identical. Unexpected however, is the modest magnitude of the spring bloom relative to the high availability of ambient nutrients. Nitrate, phosphate and silicate concentrations remained well above limitation throughout the spring season, decreasing to a minimum of 18.4, 1.2 and 32 mM respectively (Goeyens et al. 1991; van Bennekom et al. 1991). Such a low build up of biomass cannot be ascribed to low temperature stress on phytoplankton physiology, as photosynthetic and growth capacity at temperatures ranging from −1.8 to +2°C were of the same order of magnitude as those of phytoplankton in temperature waters (Lancelot et al. 1991). Hence it is likely that other factors were preventing massive biomass development in

this part of the circumpolar marginal ice zone, as discussed below.

Phytoplankton bloom development, the density field and the light environment. Stability caused by melting of ice has often been shown to be a necessary condition for the initiation of phytoplankton ice-edge blooms (Smith and Nelson 1985, 1986; Sullivan et al. 1988). The relationship between phytoplankton bloom development in the upper mixed layer and the density field of surface waters, as observed during the perpendicular section in the marginal ice zone of early summer (Fig. 3), strongly suggest that vertical stability is a necessary but otherwise not a sufficient condition to allow high biomass development. Obviously, the strong vertical stability of surface waters with about 20% ice-cover (Fig. 3) maintained itself very well in the recently ice-free area over a distance of about 250 km

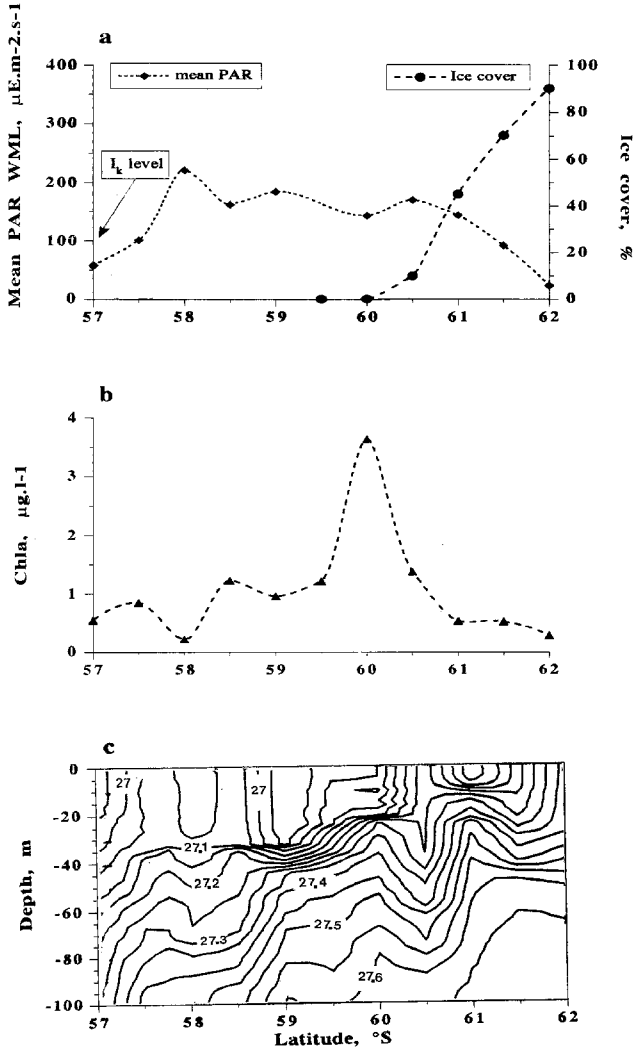

Fig. 3a–c. Field data of a north-south section along the 49°W meridian, late December: (**a**) Photosynthetically available radiation (PAR) averaged over the depth of the mixed layer and ice cover; (**b**) chlorophyll *a* concentration averaged over the upper mixed layer (Jacques and Panouse 1991) and (**c**) density field depicted by isopycnals of $\sigma\theta$ with interval of 0.05 (Veth et al. 1992)

(approaching the maximum winter sea ice extent around this meridian). In contrast, the corresponding chlorophyll *a* concentrations exhibited variations of one order of magnitude around a marked phytoplankton peak of 4 mg m^{-3} occurring at latitude 60°S (Fig. 3). Comparison of this average light levels in the upper mixed layer as calculated from incident PAR, ice-cover and the vertical light extinction coefficient (Fig. 3) highlights the dual rôle of ice-melting in initiating phytoplankton blooms by providing optimal light conditions to phytoplankton cells, due both to the creation of a shallow vertically stable environment as well as the progressive removal of sea ice (Fig. 3). At ice-coverage higher than about 40% phytoplankton development is prevented due to light limitation despite the relatively shallow upper mixed layers (Fig. 3a,b). In such areas, subsurface irradiance is greatly reduced by sea ice albedo to values below the light saturation level of 100 μE m^{-2} s^{-1}, typical of phytoplankton cells growing in this sector of the Southern Ocean (Lancelot et al. 1991). Consequently, very low chlorophyll *a* concentrations (<0.5 mg m^{-3}) are characteristic of these ice-covered areas, regardless of the vertical stability (Fig. 3c).

In most marginal ice areas, the geographical extent of blooms has been related to that of vertical stability, i.e. the persistence of near optimum light, whilst its decline has been attributed to dilution due to the northward degradation of the shallow upper mixed layer by either vertical or lateral mixing (Smith and Nelson 1985; Sullivan et al. 1988; Mitchell and Holm-Hansen 1990). Deepening of the upper mixed layer might well explain the low chlorophyll *a* concentrations typical of the permanently ice-free area north of latitude 58° S (Fig. 3b,c). In contrast, the recently ice-free zone (between 58 and 60.5°S) exhibited a persistent vertical stability seawards from the ice-edge, providing near optimum light for phytoplankton (Fig. 3a,c). Hence, other factors than deep mixing appear to be responsible for the bloom decline at latitude 59.5°S in this period.

The role of trace metals. The hypothesis that Southern Ocean phytoplankton bloom is limited by deficiency of a trace metal, notably iron (Fe), was recently suggested by Martin and Fitzwater (1988) who extrapolated from bioassays conducted in a similar high nutrient region – the subarctic North Pacific Ocean (Martin and Fitzwater 1988; Coale et al. 1991). This iron-limitation hypothesis was tested in a suite of five experimental runs in different sub-areas of the studied sector of the marginal ice zone (de Baar et al. 1990; Buma et al. 1991). Despite a clear stimulation of chlorophyll *a* synthesis in very single experiment due to Fe addition, the control bottles (no addition) also rapidly outgrew the levels of chlorophyll *a* in the field (Fig. 4). This indicated the presence of enough dissolved Fe to sustain some growth, as later confirmed by measured Fe concentration (>1 nM) in the Weddell/Scotia Sea region and upstream Peninsula waters (Nolting et al. 1991; Westerlund and Öhman 1991; Martin et al. 1990). Hence the Weddell-Scotia region of the EPOS study is not Fe-limited per se, rather Fe plays a minor role and the moderate ice-edge blooms observed here are mostly controlled by loss terms. Grazing control appears one of the

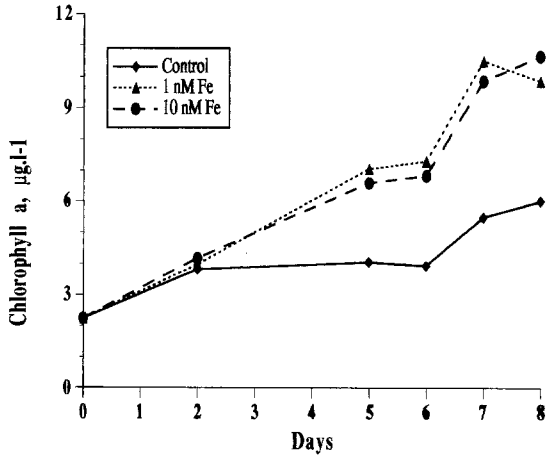

Fig. 4. The response (as Chl *a*) of the plankton community collected at 59°S, 49°W after enrichment of incubations at t=2 days with Fe=1 nM and Fe=10 nM, as compared to an untreated control (after de Baar et al. 1990)

more defensible hypotheses as low sedimentation rates of 0.005–0.03 d^{-1} were actually calculated from sediment trap data (G. Cadée, pers. com. 1991).

The role of grazing pressure. The sustained grazing pressure exerted by protozoa. Microscopical analysis of the planktonic community revealed the general dominance of nanoplanktonic forms, both autotrophs and heterotrophs, forming an overall complex microbial network characterized by strong mutual trophic relationships (Becquevort et al. 1992). Figure 5 shows the geographical variations of biomass and activity of auto- (Fig. 5a) and heterotrophic (Fig. 5c) microorganisms in the marginal ice zone of the northwestern Weddell Sea. It clearly shows that the magnitude of the developing ice-edge phytoplankton bloom is controlled by the grazing pressure exerted by protozoa that develop at the same time as phytoplankton. At the height of the bloom, protozoa represent as much as 40% of the phytoplankton biomass (Fig. 5a,c), and calculated grazing rates were higher than primary production (Fig. 5d). The collapse of the bloom, however, would be due to the combined effect of protozoa grazing pressure and deep mixing, the latter process considerably diluting phytoplankton concentrations (Fig. 5). The relative contribution of the biological versus the physical processes to the observed decrease of phytoplankton concentration thus appears to be dependent on the local meteorological conditions.

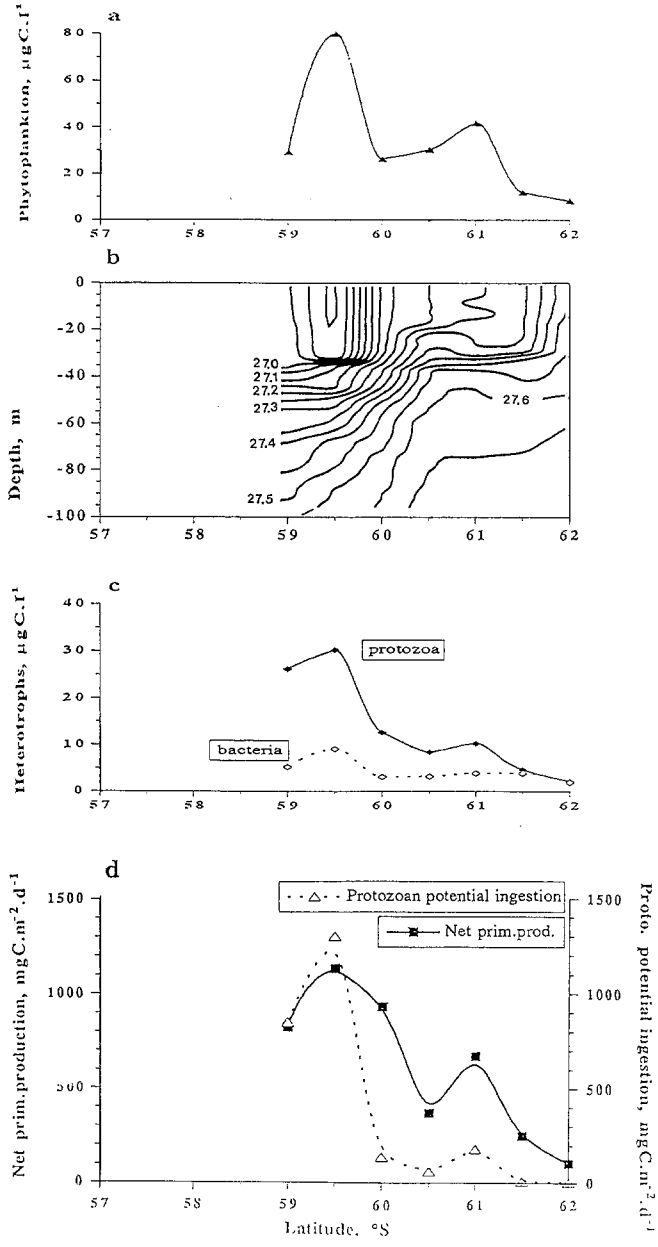

Fig. 5a–d. Field data of a north-south section along the 49°W meridian in mid-December: (**a**) phytoplankton carbon biomass averaged over the depth of the mixed layer (after Becquevort et al. 1992); (**b**) density field (after Veth et al. 1992); (**c**) heterotrophic carbon biomass (bacteria and protozoa) averaged over the depth of the mixed layer (after Becquevort et al. 1992) and (**d**) daily auto- and heterotrophic activities (after Mathot et al. 1992)

The episodic role of krill. The Antarctic krill *Euphausia superba* is one of the major components of mesozooplankton in the sea ice-associated area of the Southern Ocean (Hempel 1985). Recent studies (Smetacek et al. 1990; Siegel et al. 1990) have provided evidence that krill lives under the ice during winter, shifting to a pelagic mode of life in summer. By alternatively exploiting sea ice algae and phytoplankton, krill might control the phytoplankton ice-edge bloom at different stages during the course of its development. Overwintering krill in the pack ice-zone is likely to have a predominant effect on phytoplankton ice-edge bloom initiation and magnitude. The krill is thought to reduce initial stocks by scraping the ice, particularly at the time of ice melting, when sea ice algae are released in the water column (Marshall 1988; Stretch et al. 1988; Smetacek et al. 1990). During EPOS, high krill biomass (1–27 $g\,m^{-2}$) was recorded in the closed pack ice-zone of the Weddell Sea in the early beginning of the ice melting process (Siegel et al. 1990). The strong taxonomic dissimilarity observed between sea ice assemblages and adja-

cent water column phytoplankton, sampled simultaneously in the studied area (Mathot et al. 1991b) and the presence of numerous krill swimming around ice floes strongly suggest that a major portion of sea ice algae released in the water column quickly disappeared through krill grazing. Accordingly, a low seeding stock of 0.05 mg Chl $a\,m^{-3}$ was calculated by Lancelot et al. (1991) from empirical relationship relating chlorophyll *a* concentration to ice-cover. Formation of sea-ice algal aggregates characterized by a subsequent high sedimentation rate may be an additional factor eliminating ice algae during melting (Riebesell et al. 1991). The relative importance of these processes in controlling seeding of the water column needs further investigation.

In its pelagic mode, krill is able to travel large distances, literally clearing the water column by grazing on meso- and micro-organisms. During the 70-day EPOS expedition only one krill passage was recorded (Hempel et al. 1989). Its impact on phytoplankton was most dramatic, reducing chlorophyll *a* concentrations from 2.5 $mg\,m^{-3}$ to 0.3 $mg\,m^{-3}$ within two to three h while changing the phytoplankton species composition from a diatom- to a nanoflagellate-dominated population (Jacques and Panouse 1991).

Mathematical modelling

Basic statements. The above examination of the factors controlling the phytoplankton bloom development in the marginal ice zone of the northwestern Weddell Sea leads us to support Mitchell et al. (1991) and Sakshaug et al. (1991)'s hypothesis that phytoplankton bloom development in the Southern Ocean is highly sensitive to both physical and biological parameters that determine vertical mixing and phytoplankton loss rate. Our data clearly show that bloom initiation is mainly under the control of physical processes that determine the vertical stability of surface waters. Grazing pressure actively controls both the magnitude and extent of the bloom, thus preventing the occurrence of massive phytoplankton blooms in this sector of the circumpolar marginal ice zone. Protozoa exert a semi-continuous control on phytoplankton development while the role of krill, due to its life history, is more episodic. Krill affects phytoplankton ice-edge blooms in two ways. Overwintering krill reduces and modifies the sea-ice algal seeding input into the water column. During their swarning migrations later in the season, the krill is responsible for randomly occurring but intensive grazing on the then more developed algal blooms. Neither the major nutrients nor the trace metals appear to exert a significant direct control on the magnitude of the phytoplankton ice-edge bloom in this region and season. However, an indirect role of trace metals in controlling phytoplankton development cannot be totally excluded. The dominance of small fast-growing phytoplankton cells which in turn are efficiently grazed by protozoa could be interpreted as a result of iron limitation (Morel et al. 1991).

The mathematical model. To what extent physical and biological factors interact in generating and controlling phytoplankton blooms in the circumpolar marginal ice zone of the Southern Ocean was investigated through a suite of simulation runs with the coupled physical-biological model of Lancelot et al. (1991) applying to various realistic weather and grazing pressure scenarios. This one-dimensional two-layer ecological model calculates the development of phytoplankton bloom as a function of phytoplankton physiology, depth of the wind-mixed layer, irradiance and phytoplankton loss rates. No net horizontal advection is considered due to its large time scales compared with the other terms in the model. This model was established on the basis of field observations and process studies as described in Lancelot et al. (1991). It differs from those developed by Mitchell et al. (1991) and Sakshaug et al. (1991) in that (i) the dynamics of sea ice retreat is considered, (ii) phytoplankton loss terms as respiration and grazing pressure are explicitly described and (iii) the temperature dependence of some physiological parameters has been assessed (Lancelot et al. 1991). The physical model (Veth 1991) is a one-dimensional turbulent hydrodynamical model with measured meteorological and ice conditions as its forcing variables. The model of phytoplankton development is based on the concept of energy storage theory (Cohen and Parnas 1976) for an adequate description of the interaction between phytoplankton physiology and light fluctuations due to vertical mixing. The rates of photosynthetic, growth, respiration and excretion rates are explicitly calculated on the basis of parameterizations of the knowledge of various regulatory mechanisms (AQUAPHY model, see equations and parametrization in Lancelot et al. 1991). Control by protozoa is represented by a temperature-dependent linear equation (Lancelot et al. 1991) while krill is considered as a random external constraint. Losses by sedimentation are neglected due to their low impact (0.005 to 0.03 d^{-1}) compared to grazing (0.01 to 0.3 d^{-1}). Also, inorganic nutrients and trace elements, not being considered as limiting factors of phytoplankton development in this section of the circumpolar marginal ice zone, are ignored.

Model simulations. Model simulations were run for latitude 59.5°S within the marginal ice zone of the northwestern Weddell Sea during spring. The 70-day simulated period at this latitude covers the complete ice-melting period as well as the subsequent one-month ice-free period (Fig. 6), thus illustrating over time the sea ice retreat by including the remnant effect of ice melting on the stability of ice-free surface waters (Veth et al. 1992).

Highly fluctuating weather conditions occurring at scales of shorter than one week are typical for the Southern Ocean (Deacon 1984). Short-term extreme wind fluctuations of between 2 and 17 $m\,s^{-1}$ around an average value of 8 $m\,s^{-1}$ were observed during the studied period (Fig. 6c). Solar radiation fluctuated similarly giving rise to periods of sunny days with little wind alternating with cloudy days and strong wind. These fluctuations have a dramatic influence on the predicted depth of the upper mixed layer, which varies between 4 and 70 m, as an indirect response to diurnal fluctuations of wind speed and solar radiation (Fig. 6d). The frequency, duration and strength of mixing events were particularly important

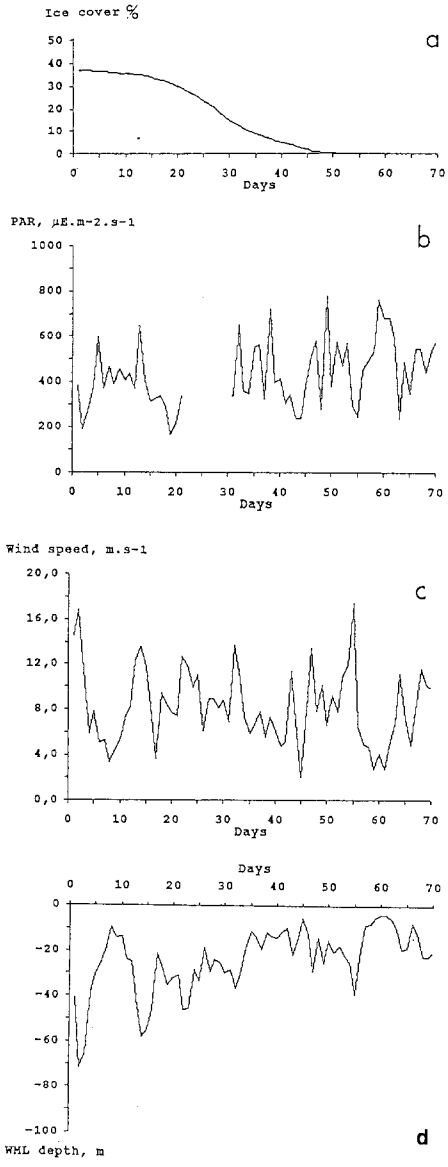

Fig. 6a–d. The seasonal fluctuation of physical variables at latitude 59.5°S from 26th October to 31th December 1988: (**a**) ice-cover; (**b**) averaged photosynthetic available radiation at the sea surface; (**c**) wind speed daily average and (**d**) predicted depth of the upper mixed layer from above meteorological parameters (after Veth, 1991)

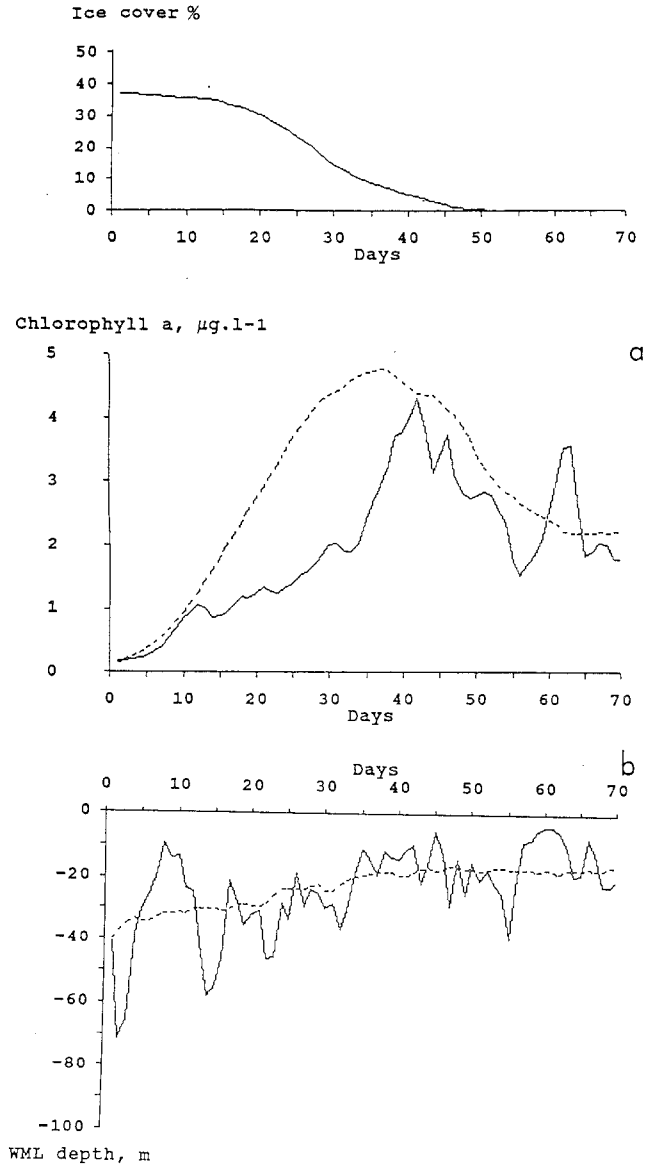

Fig. 7a, b. Simulated response at latitude 59.5°S under local (*solid line*) and averaged (*dotted line*) meteorological conditions: (**a**) simulated chlorophyll *a* concentration of the upper mixed layer; (**b**) simulated upper mixed layer

during the ice-covered period which was characterized by an alternation between short terms with a shallow upper mixed layer (5 to 30 m) and longer time spans with deep vertical mixing (depths exceeding 50 m). Due to the high friction coefficient of ice, the layer affected by transient wind events was, on average, deeper within the ice-covered period (70 m) than after melting of the ice (38 m; Fig. 7). The extent to which such episodic wind events affect sea ice-associated phytoplankton bloom development is shown in Fig. 7 and 8 which compare temporal evolution of surface layer phytoplankton as predicted for different weather scenarios. Comparison of simulations generated by local weather conditions and those averaged over the 70-day simulated period brings out the importance of deep mixing events in delaying the build up of phytoplankton biomass in the ice-covered domain. In this area, light penetration is considerably reduced by sea ice albedo and local shallow upper layer events were insufficient for counterbalancing deep mixing which dilutes the phytoplankton concentration in a lower irradiance environment. This is the consequence of the asymmetrical behavior of the wind mixed layer in terms of deepening and shallowing. Deep mixing is accompanied by vertical dilution of phytoplankton, whereas shallowing of the mixed layer does not reconcentrate the phytoplankton back into the upper waters. This asymmetry of a single deep-mixing event has dramatic consequences for the initiation of the phytoplankton bloom. During the EPOS expedition in particular, the successive wind mixing events

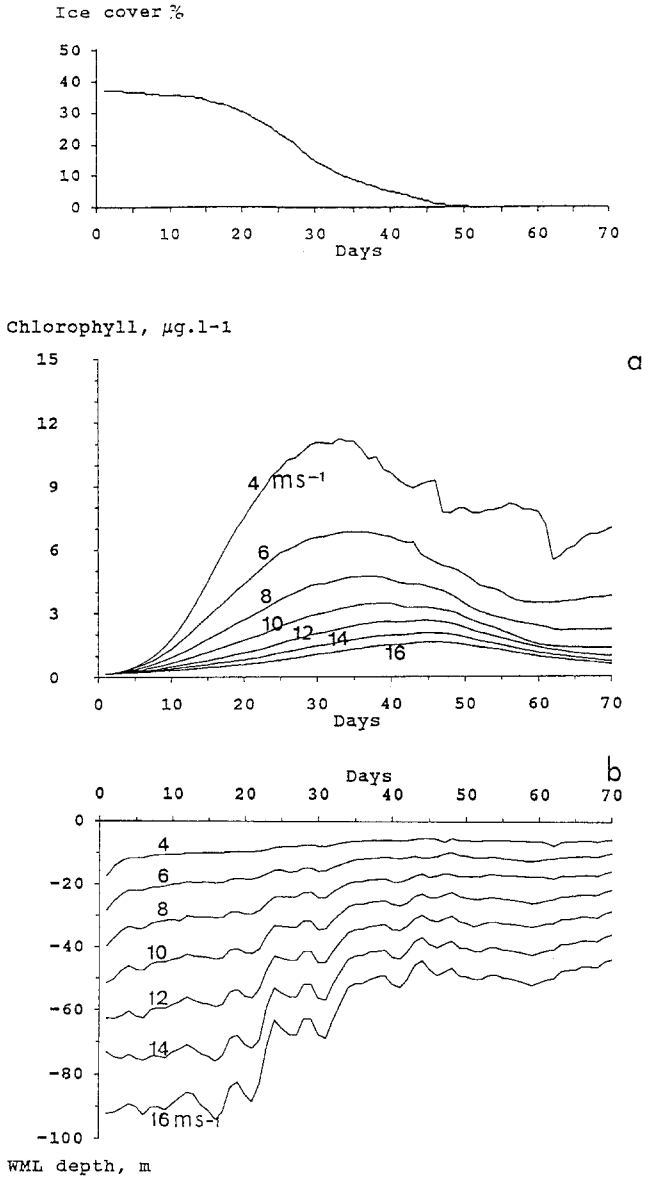

Fig. 8a, b. Simulated response at latitude 59.5°S to different constant wind speeds ranging from 4 m s^{-1} to 10 m s^{-1}, for given percentage ice-cover (see Fig. 6 for ice-cover): (**a**) simulated Chl *a* concentration of the upper mixed layer; (**b**) simulated upper mixed layer

occurring during the ice-covered period considerably delayed the exponential development of phytoplankton as well as its maximum appearance with respect to that predicted under constant averaged wind conditions (Fig. 7). Similar maximum chlorophyll *a* concentrations of about 4.5 mg m^{-3} are predicted by both scenarios (Fig. 7).

The role of wind velocity on phytoplankton ice-edge bloom development and magnitude is shown in Fig. 8, which compares chlorophyll *a* concentrations predicted under various constant wind regimes. These simulations show that, depending on the wind speed, the phytoplankton peak appearance shifts with respect to ice-cover, occurring between 0 and 20% of the latter. More spectacular is the range of maximum phytoplankton concentration predicted, varying from 1.5 to 11 mg Chl *a* m^{-3} (Fig. 8).

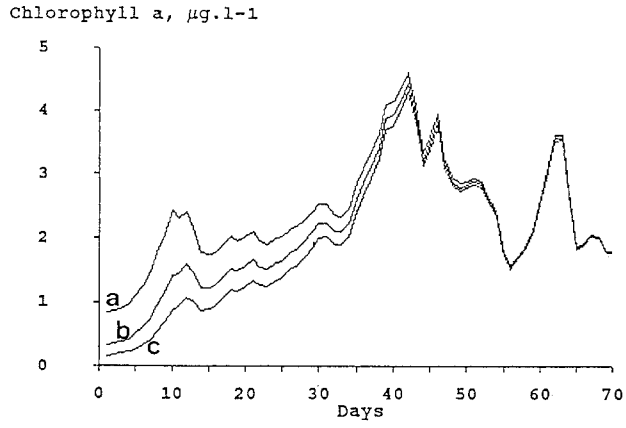

Fig. 9. Simulation at 59.5°S of the Chl *a* concentration of the upper mixed layer, in response to various seeding scenarios: (*a*) 0.8; (*b*) 0.4; (*c*) 0.1 mg Chl *a* m^{-3}. Percentage ice-cover and other forcing variables as in Fig. 6

Under a constant wind of 14 m s^{-1}, no real phytoplankton bloom is predicted.

The role of seeding in generating ice-edge blooms was studied by comparing simulations which were run with various initial concentrations of phytoplankton corresponding to a realistic range of seeding concentrations. Latter values had been roughly calculated from chlorophyll *a* concentrations measured in sea-ice floes (Garrison 1986) diluted within the upper mixed layer at initial conditions, by assuming an ice floe average diameter of 20 m at the time of melting (van Franeker, pers. comm. 1991) and a preferential peripheral distribution of sea-ice communities. Simulations (Fig. 9) clearly show that seeding solely affects the early development of phytoplankton during the ice-covered period by allowing the occurrence of sporadic minor blooms. The frequency and magnitude of these blooms are related to weather conditions. Seeding does not affect the predicted peak appearance and maxima reached by the ice-edge bloom.

The role of protozoan grazing pressure in determining the height and magnitude of the ice-edge phytoplankton bloom is shown by analyzing predictions resulting from elimination of protozoan grazing pressure (Fig. 10). While not significant during the early development of phytoplankton, losses by grazing do lower the maximum concentration of the sea ice-associated bloom i.e. 60% lower than without grazing (Fig. 10). Hence the chlorophyll *a* concentration of 7.5 mg m^{-3}, predicted by excluding grazing, represents the maximum ice-edge phytoplankton biomass to be reached under local meteorological conditions. The extent of the ice-edge bloom on the other hand is clearly determined by the balance between phytoplankton losses due to grazing pressure and the persistence of optimal light conditions due to favorable wind conditions. Phytoplankton decline is predicted under the observed grazing pressure, whereas bloom development would have persisted in absence of grazers (Fig. 10).

Most scenarios predict a steady-state phytoplankton concentration in the summer, the magnitude of which greatly depends on weather conditions (Figs. 7 and 8) and

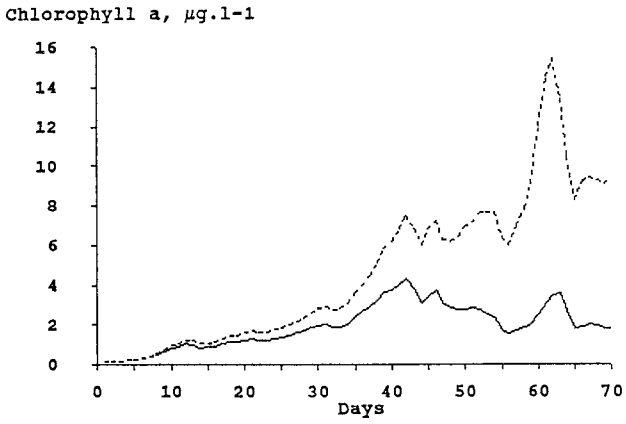

Fig. 10. Simulation at 59.5°S of the Chl *a* concentration of the upper mixed layer with (*solid line*) or without (*dotted line*) grazing pressure by protozoa. Percentage ice-cover and other forcing variables as depicted in Fig. 6

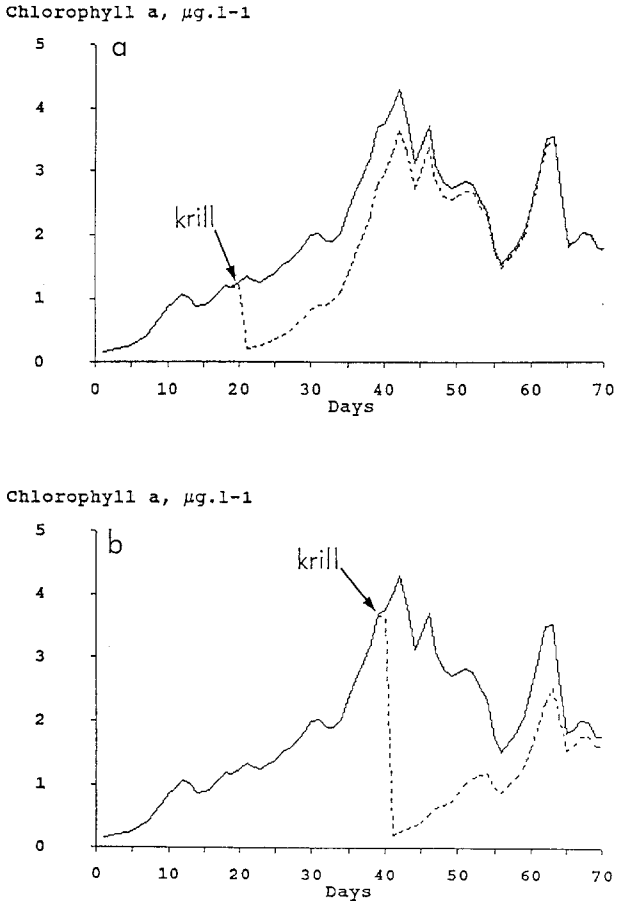

Fig. 11a, b. Simulation at 59.5°S of the Chl *a* concentration of the upper mixed layer without (*solid line*) or after a randomly occurring krill grazing event (dotted line), here chosen at (**a**) the initial stage or (**b**) blooming stage (t = 40 d) of phytoplankton development. Percentage ice-cover and other forcing variables and as in Fig. 6

grazing pressure (Fig. 10). The occurrence of secondary phytoplankton peaks during the ice-free period, as predicted around day 60 (Fig. 10), is clearly related to the amplitude and duration of wind mixing events. Indeed no such summer development is predicted by constant wind scenarii (Fig. 8). Whereas the height of these secondary phytoplankton blooms is determined by both the grazing pressure and the persistence of vertical stability providing favorable light conditions to phytoplankton, their decline is mostly due to vertical dilution of phytoplankton into a lower irradiance field (Fig. 7).

The impact of krill swarm passages on the development of sea ice associated phytoplankton blooms is determined by its occurrence with respect to the phytoplankton bloom development stage (Fig. 11). A krill event occurring under the ice (Fig. 11a) has little influence on the chlorophyll *a* biomass prediction associated with the ice melting process and no effect on secondary blooms resulting from stable wind mixing events. Conversely a krill passage at the blooming stage eliminates the bloom and controls the magnitude of secondary summer peaks (Fig. 11b).

Conclusions

Physical, chemical and biological data collected in the marginal ice zone of the northwestern Weddell Sea during sea ice retreat 1988 give additional support to Mitchell et al. (1991) and Sakshaug et al. (1991)'s hypothesis of a control of phytoplankton blooms development in the Southern Ocean by physical and biological parameters governing vertical mixing and phytoplankton losses. Fe was shown to play a minor role in this area of the Southern Ocean dominated by nanoplanktonic communities. Phytoplankton loss rates were mainly due to protozoa grazing whereas sedimentation rates were generally very low.

Various weather and grazing pressure scenarios applied to a one-dimensional ecological model explicitly describing the relationship between phytoplankton physiology, the physical properties of its habitat and the biological control by grazers demonstrate that initial ice-edge phytoplankton bloom development is determined by the physical properties of the surface layer, under control of meteorological conditions. The position of the phytoplankton bloom, however, shifts with respect to the ice-edge position, depending on weather conditions, most notably, the frequency, duration and strength of mixing events which considerably delay the ice-edge bloom development. The magnitude and extent of the phytoplankton bloom is, on the other hand, determined by the combined action of weather and grazing. Extreme wind conditions, i.e. 14 $m\,s^{-1}$, in combination with realistic grazing pressures, however, prevent bloom development. After the ice-edge bloom development a summer steady state is reached of which the concentration varies according to grazing pressure and mean meteorological conditions. Secondary open sea summer phytoplankton blooms can however develop depending on the occurrence of durable shallow wind mixing periods which determine their wax and wane. The intensity of these blooms is controlled by the grazing pressure.

Krill overwintering beneath the ice affects the development of early small blooms under the ice but plays no

significant role on the development of the ice-edge bloom. Conversely, the incidence of a krill passage at the time of ice-edge bloom development is dramatic, determining the disappearance of the bloom and the relative importance of summer episodic blooms created by favorable weather conditions.

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